THE TRUNK MUSCULATURE OF *SANZINA* AND ITS BEARING ON CERTAIN ASPECTS OF THE MYOLOGICAL EVOLUTION OF SNAKES

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Since Mosauer's paper in 1935,[1] very little has been published concerning the myology of the trunk region in snakes. In that paper he outlined three myological types on the basis of an examination of a number of species[2] from several distinctly related groups. These types were described as characteristic of (1) the Boidae, (2) the Colubridae and (3) the Viperidae, and were distinguished on the basis of several correlated peculiarities in muscle arrangement. These arrangements were, according to Mosauer "surprisingly constant" within each group.

As a contribution to a much needed wider survey of snake myology, the body musculature of *Sanzina* (a boid genus rarely available for this type of study) is described in this paper. It is shown that, at least in this genus, there is considerable departure from the basic boid pattern described by Mosauer. More important, this departure embodies some aspects of myological arrangement previously considered to be characteristic of the Viperidae or Colubridae.

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[1] Walter Mosauer (1935) Univ. Calif., Los Angeles. Publ. Biol. Sci., Vol. 1. No. 6, pp. 81-120.

[2] In addition to *Constrictor constrictor*, Mosauer examined the following boid genera and species: *Python molurus, Calabaria reinhardti, Epicrates striatus, Lichanura roseofusca* and *Charina bottae*.

I wish to thank Dr. Ernest E. Williams, Museum of Comparative Zoology, who made the specimen of *Sanzina* available for study. Dr. William Riemer, Florida State Museum, made it possible to study the musculature of a large specimen of *Ophiophagus hannah* in the University of Florida collections, for which I am very grateful.

The description below is based on a single adult specimen of *Sanzina madagascarensis*, approximately four and a half feet long (M.C.Z. 8002). In addition, the musculature of one specimen each of *Crotalus durissus terrificus, Ophiophagus hannah* and *Coluber constrictor* was studied. No differences were found from the descriptions of these or similar forms given by Mosauer. The myological description of *Sanzina* is meant to supplement that given by Mosauer, and follows, for the most part, his outline of presentation to facilitate comparison.

M. Semispinalis et spinalis
(Figs. 1, 4, *SSP.SP.*)

As in *Constrictor constrictor,* this muscle arises from a tendinous arch, stretching between the neural spine and postzygapophysis of a single vertebra, with the concavity directed caudally. From this arch the muscle extends as a flat ribbon, directed forward, medially and dorsally. It is inserted by a tendon into the caudodorsal edge of the neural spine of a more anterior vertebra. From origin to insertion the muscle and its tendons cover ten segments.

As in the typical boid arrangement, the medial portion of the muscle seems to represent the spinalis and the lateral part the semispinalis fused and inserted by means of a common terminal tendon.

M. Longissimus dorsi
(Figs. 1, 2, 3, 4, *ML*)

This muscle is also similar to that in *Constrictor,* with the origin at the craniolateral portion of a prezygapophysis. At about the level of the thirteenth vertebra cranial to its origin the muscle is replaced by a flat tendon, which divides in two. The medial division inserts on the posterolateral portion of the four-
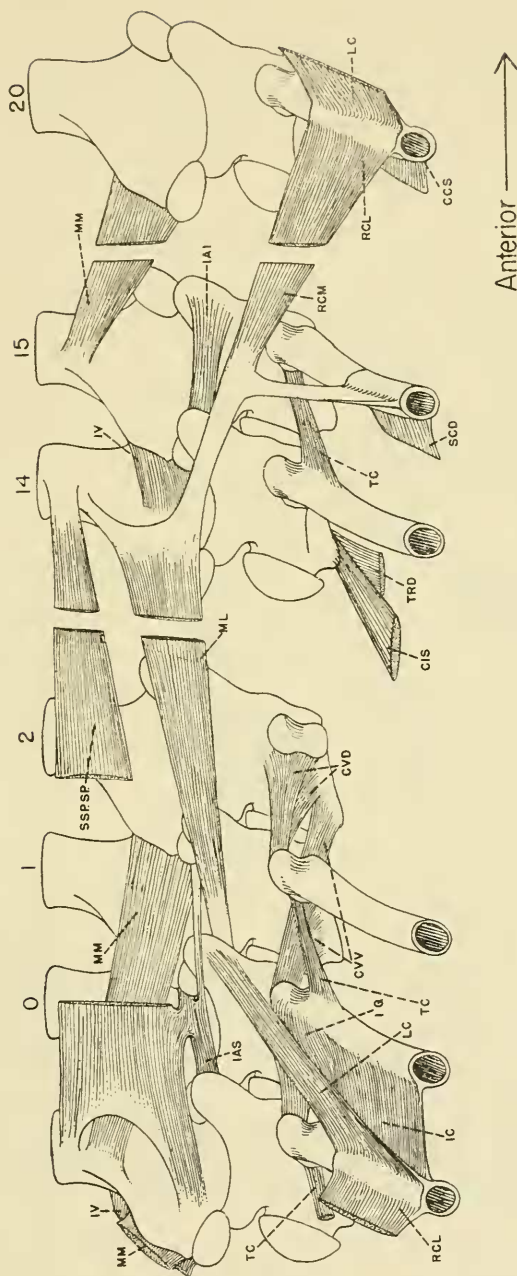
Anterior ⟶

Fig. 1. Diagrammatic lateral view of the musculature of the middle thoracic region in *Sanzina*. Gaps in the column represent missing portions and numbers over the vertebrae indicate vertebral position. Thus the longissimus passes over thirteen vertebrae to insert on the fourteenth cranial to its origin. Abbreviations: *CCS*, costocutaneus superior; *CIS*, costalis internus superior; *CVD*, dorsal head of the costovertebrocostalis; *CVV*, ventral head of the costovertebrocostalis; *IAI*, interarticularis inferior; *IAS*, interarticularis superior; *IC*, intercostalis proprius; *IQ*, intercostalis quadrangularis; *IV*, intervertebralis; *LC*, levator costae; *ML*, longissimus; *MM*, multifidus; *RCL*, lateral belly of the retractor costae biceps; *RCM*, medial belly of the retractor costae biceps; *SCD*, supracostalis dorsalis; *SSP.SP.*, semispinalis et spinalis; *TC*, tuberculocostalis; *TRD*, transversus dorsalis.

teenth neural spine anterior to the origin of the muscle. The
lower division of the tendon extends cranially for an additional
vertebra, where it sends a small thin tendinous slip to the rib of
the fifteenth vertebra, closely associated with the origin of the
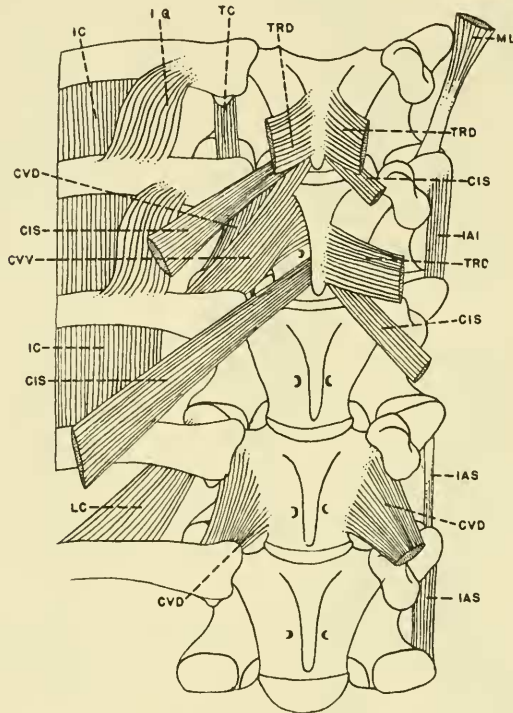
Anterior

Fig. 2. Diagrammatic ventral view of the musculature of the middle
thoracic region in *Sanzina*. Abbreviations: *CIS*, costalis internus supe-
rior; *CVD*, dorsal head of the costovertebrocostalis; *CVV*, ventral head of
the costovertebrocostalis; *IAI*, interarticularis inferior; *IAS*, interarticularis
superior; *IC*, intercostalis proprius; *IQ*, intercostalis quadrangularis; *LC*,
levator costae; *ML*, longissimus; *TC*, tuberculocostalis; *TRD*, transversus
dorsalis.

supracostalis dorsalis and the insertion of the medial belly of the
retractor costae biceps. Anterior to the fifteenth vertebra, the
aponeurosis of the longissimus gives rise to the slender, band-like

medial belly of the retractor costae, which in turn gives rise to the more anterior lateral belly, inserting on the twentieth vertebra cranial to the primary origin of the entire complex.

The main differences between this series of muscles and tendons in *Sanzina* and *Constrictor* lie in the lengths of the myological segments. In the former the medial tendinous insertion of the longissimus is on the fourteenth neural spine. In the latter it is on the ninth. In *Sanzina* the tendinous slip from the aponeurosis of the longissimus inserts on the fifteenth rib; in *Constrictor* it inserts on the fifth. The entire complex, including the lateral head of the retractor costae includes twenty vertebrae in *Sanzina,* and eighteen in *Constrictor.* Thus, the longissimus is five segments longer in *Sanzina,* and the retractor costae biceps complex seven segments shorter.

M. Multifidus
(Figs. 1, 4, *MM*)

In *Constrictor* this muscle originates from the ventral surface of the tendinous arch forming the origin of the semispinalis et spinalis. It extends four to five segments, inserting into the caudal border of the laminae of the neural arch. In *Sanzina,* as in most Colubridae and Viperidae studied by Mosauer, the muscle arises from the craniodorsal edge of the neural spine, and as in *Crotalus* extends anteriorly for only three to four vertebrae.

M. Interarticularis superior
(Figs. 1, 2, 3, 4, *IAS*)

In *Constrictor* this muscle arises from the lateral tendon of the tendinous arch of the semispinalis et spinalis. It then extends anteriorly for four vertebrae, where it inserts on the posterior lateral border of the postzygapophysis of several successive vertebrae. In *Sanzina* the muscle originates on the craniodorsal border of the postzygapophysis and extends cranially for one vertebra, inserting on the same region as in *Constrictor.* The muscle is thus considerably shorter in *Sanzina,* being similar to that in the Viperidae. In addition, its origin on the postzygapophysis, rather than on the tendinous arch suggests the condition Mosauer found in most colubrids and viperids. On the other

hand, the muscle is joined by a slip from the lateral portion of the fused semispinalis et spinalis, suggesting the origin for the interarticularis superior found in most boids (Fig. 4, A, B).

Mosauer takes the medial head of the digastricus dorsalis of Colubridae to be homologous with the interarticularis superior of the Boidae. In all of the colubrid genera which he studied the medial head of the digastricus arises from the superior surface of the postzygapophysis and inserts by a thin tendon into the caudal border of a postzygapophysis several vertebrae cranially. It is joined by the lateral head of the digastricus, which arises from the accessory process of the next vertebra posterior to the one which forms the origin of the medial head. It is also joined by a small raphe of the longissimus (Fig. 4, D).

In *Sanzina* the main body of the interarticularis superior inserts on the cranial border of the postzygapophysis of the preceding vertebrae as in other boids, but a small tendinous slip passes cranially to a slightly more lateral insertion on the postzygapophysis of the second preceding vertebra. This tendon is so similar to the anterior tendon of the digastricus in most colubrids that there can be little doubt as to homology.

In the Anilidae, according to Mosauer, the medial head of the digastricus arises on the tendinous arch of the semispinalis et spinalis. It joins the lateral head, which covers one vertebra, and is apparently homologous to the interarticularis superior of *Sanzina*.

Mosauer states that in the colubrid snakes the lateral head of the digastricus has apparently migrated posteriorly to the accessory process of the succeeding vertebra, and has also become associated by means of a small raphe with the longissimus of the succeeding vertebra. That such migration is possible in the Colubridae seems reasonable in view of the fact that in at least the single specimen of *Coluber* which I have examined the lateral head of the digastricus is provided with a very thin tendon connecting that muscle with the superior surface of the postzygapophysis; probably this tendon represents the caudal end of the interarticularis superior of the Boidae. The caudal tendon of the medial head of the digastricus thus seems to represent, at least in part, the original semispinalis et spinalis of the tendinous arch.

It seems reasonable to assume that the semispinalis has mi-

grated posteriorly along the medial tendon of the longissimus. The Anilidae apparently represent an intermediate condition (Fig. 4).

In the Viperidae the interarticularis superior is said by Mosauer to be very similar to that in the Boidae, except that a few fibers originate on the postzygapophysis. I have checked this in *Crotalus durissus terrificus*. The muscle extends for only one
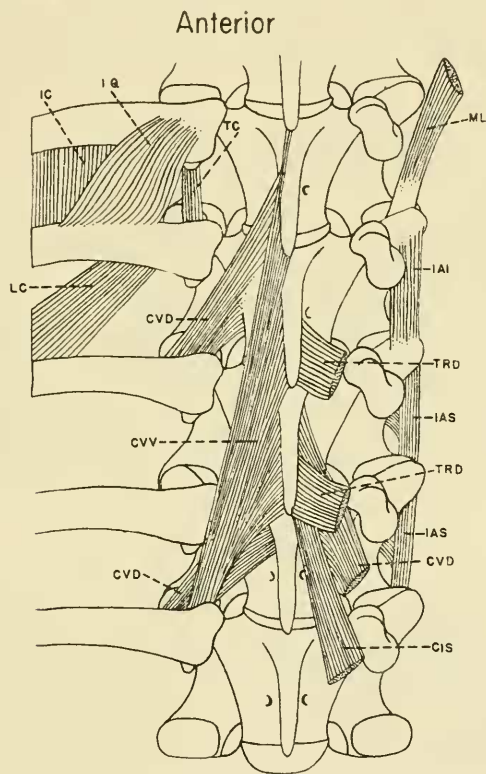
Anterior

Fig. 3. Diagrammatic ventral view of the musculature of the anterior thoracic region in *Sanzina*. Abbreviations as in Figure 2.

vertebra, as the main portion does in *Sanzina*. However, in *C.d. terrificus* and in the other viperids examined by Mosauer there is no anteriorly directed tendon, and the muscle originates mainly on the semispinalis et spinalis.

M. Costovertebrocostalis
(Figs. 1, 2, 3, *CVD, CVV*)

As in *Constrictor,* this muscle is composed of two heads. The medioventral head arises from the lateral surface of the haemal keel and from the caudoventral parapophysial portion of the paradiapophysis. It extends caudally and laterally, inserting on the costal tubercle and neck of the succeeding rib. The dorsal head arises from the cranioventral portion of the diapophysial portion of the paradiapophysis and unites with the ventral head caudally.

M. Intercostalis quadrangularis
(Figs. 1, 2, 3, *IQ*)

This small muscle is not mentioned by Mosauer in his description of the typical musculature of the Boidae, but only in the description of the arrangement found in the Colubridae. It is, however, well developed in *Sanzina*. As in the Colubridae and Viperidae, it arises from the caudal surface of the capitulum costae, just lateral to the articular head of the rib, running caudally and laterally to be inserted on the inferior cranial border of the following rib. The identity of this muscle in *Sanzina* is so obvious that homology to the similar muscle mass in the Colubridae is hardly to be questioned.

M. Tuberculocostalis
(Figs. 1, 2, 3, *TC*)

Mosauer describes this muscle as being found only in the Colubridae. However, it is present in *Sanzina,* originating, as it does in colubrid snakes, from the laterocaudal circumference of the dorsocaudal costal tubercle, running obliquely to insert on the cranial border of the neck of the following rib.

OTHER MUSCLES

In addition to the muscles described above, the remaining units described by Mosauer as being found in the Boidae have all been located in *Sanzina*. Some of these differ in a very minor fashion from those found in *Constrictor*. The retractor costae biceps is

somewhat shorter, as pointed out above. The costalis interni superior covers eight vertebrae in *Sanzina* and nine in *Constrictor*. The following muscles were found to be the same in both *Constrictor* and *Sanzina:* Intervertebralis, levator costae, transversus dorsalis, interarticularis inferior, supracostalis dorsalis,
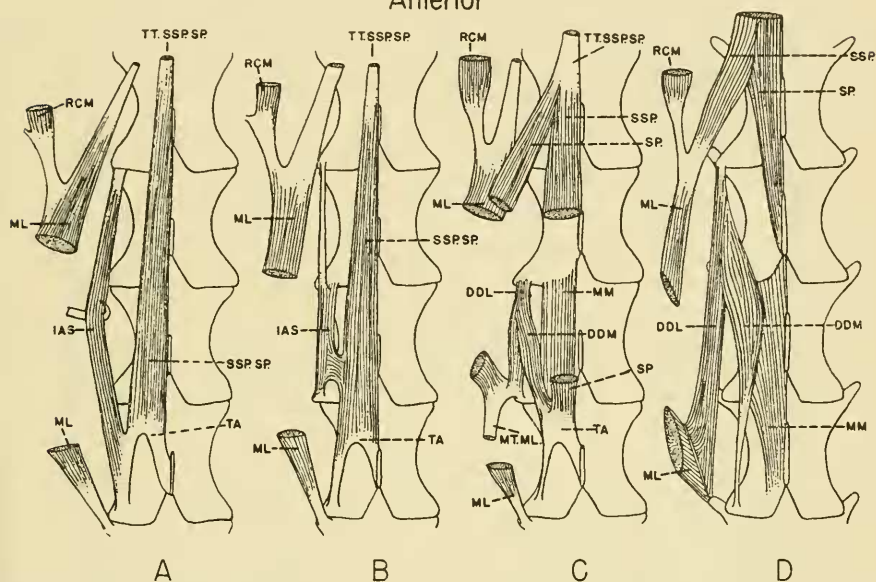

Fig. 4. Diagrammatic representations of the dorsal musculature of (A) *Constrictor*, (B) *Sanzina*, (C) *Anilius* and (D) *Coluber* illustrating the apparent evolution of the semispinalis et spinalis and the interarticularis superior to form the digastricus and the highly modified semispinalis in the Colubridae. Abbreviations: *DDL*, digastricus, lateral head; *DDM*, digastricus, medial head; *IAS*, interarticularis superior; *ML*, longissimus; *MM*. multifidus; *MT. ML.*, median tendon of the longissimus; *RCM*, retractor costae biceps, medial belly; *SP*, spinalis; *SSP*, semispinalis; *SSP.SP.*, semispinalis et spinalis; *TA*, tendinous arch; *TT. SSP.SP*, terminal tendon of the semispinalis et spinalis.

supracostalis lateralis superior, supracostalis lateralis inferior, intercostalis proprius, intercartilaginosus, costalis inferior, transversus abdominus, obliquus abdominis internus, costocutanus superior and costocutanus inferior.

COLUMNAR VARIATION

Little work has been done regarding the change in position and shape of muscles from the middle to the anterior or posterior portion of the vertebral column in snakes. Considerable structural changes take place along the length of the column. The most important of these is the presence of well-developed hypapophyses anteriorly. Such changes would be expected to influence arrangement of at least some myological elements in the anterior part of the column. Mosauer made only a few comments concerning this variation.

For the most part, myological changes correlated with intercolumnar morphological variability involve shortened or lengthened muscle segments, so that fewer or additional vertebrae are covered in the anterior part of the column than in the middle or posterior portions. However, some of the changes involve more than mere variability in muscle length, and these are of considerable interest (cf. Figs. 2 and 3).

As mentioned previously, and also by Mosauer, the transversus dorsalis is apparently absent in the anterior part of the column of most snakes. The costalis internis superior thus forms the inner muscular lining of the body cavity in this region. The latter muscle becomes progressively shorter and thicker cranially, so that each muscle covers only three segments instead of eight as in the mid-dorsal region. The insertion and origin, as well as relationship to other muscles, remain the same.

Of the deeper muscles the costovertebrocostalis becomes longer anteriorly, covering from one to four vertebrae, instead of only one to two. Occasional fibers may even extend to the fifth vertebra anteriorly. As in the middle thoracic region, the muscle is provided with two heads. The longer, thinner member inserts on the cranioventral portion of the hypapophysis of the fourth vertebra cranially. The shorter, thicker head inserts on the basal part of the hypapophysis and the ventrolateral portion of the body of the centrum, including the cranial border of the parapophysis. Of particular importance is the fact that in this area this muscle also originates in two heads, the larger on the neck of the rib, and the smaller on the cranial surface of the parapophysis. The fibers of both become interlaced before they divide into the two heads at their insertions described above (Fig. 3).

Mosauer described a muscle, the transversohypapophyseus, supposedly peculiar to the Colubridae, Elapidae and Viperidae, which originates on the cranial border of the parapophysis and extends to the caudolateroventral border of the hypapophysis. These fibers are also joined by others from deeper, shorter muscle segments. The muscle is quite distinct in the single specimens of *C. constrictor, Ophiophagus hannah* and *C. durissus terrificus* I have examined. It seems highly probable that the same muscle is represented in the anterior portion of the vertebral column of *Sanzina* as a second head of the costovertebrocostalis, not fully separated from a shorter head, which lies ventral to it (Figs. 2, 3), and which is found as a distinct unit in the anterior vertebrae of the Colubridae and all vertebrae of the Viperidae and Elapidae. Mosauer also reports the transversohypapophyseus as extending to the anus in colubrids in which hypapophyses are present throughout the column. Thus it seems apparent that the muscle cannot be considered characteristic of any particular family or families, but simply a development of the costovertebrocostalis found only in those regions of the column in which hypapophyses are well developed.

DISCUSSION

The exact phyletic position of *Sanzina* is not at all clear and the present myological study sheds little light on this problem. The genus is generally placed in the Boinae. Its zoogeographic isolation on Madagascar suggests that it may represent a very old stock.

Myologically *Sanzina* is not as much like *Constrictor* as one would suppose. Deviations in muscular arrangement are suggestive of intermediacy between typical boines, such as *Constrictor*, and the Anilidae, as represented by *Anilius*. The latter seems, in turn, intermediate between *Sanzina* and the Colubridae.

It is entirely possible that various members of the Boidae have independently evolved colubrid-like modifications several times in the past. These radiations may even be represented in rather extreme fashion by one or more of the Recent morphologically intermediate families (Anilidae, Xenopeltidae and Uropeltidae). *Sanzina*, as a slightly modified general boid type, may represent a single minor radiation paralleling the myo-evolutionary se-

quence leading to the Colubridae. There is, at least at present, little reason to suppose that *Sanzina* is on, or even close to, the line leading to the colubrids.

The musculature of relatively few snakes is known in detail. Before the full value of this tool in systematics can be realized, it is necessary to study the myology of many important Recent genera. Mosauer had intended that his observations would stimulate other workers to examine more closely the trunk musculature of snakes. However, the preliminary nature of his study has been largely overlooked by later writers. It is hoped that the present paper will re-awaken interest in comparative trunk musculature of reptiles if only by pointing out the inadequacy of Mosauer's system, which was intentionally over-simplified because of its admitted preliminary nature.